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Global stability and persistence in LG-Holling type-II diseased predators ecosystems

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Abstract

A Leslie-Gower Holling type-II model is modified to introduce a contagious disease in the predator population, assuming that disease cannot propagate to the prey. All the system's equilibria are determined and the behaviour of the system near them is investigated. The main mathematical issues are global stability and bifurcations for some of them, together with sufficient conditions for persistence of the ecosystem. Counterintuitive results on the role played by the intraspecific competition are highlighted.

1 Introduction

Ecoepidemiology merges two important fields in biomathematics, namely demographic systems, in which two populations interact either by competition or associate for mutual benefit, and models in which the spread of diseases is studied. In ecoepidemiology namely at least one disease affects one of two or more interacting populations. Since diseases insurge commonly among human and animal populations, to assess the role they play in the evolution of ecosystems becomes a relevant issue. Furthermore, to fight and eradicate diseases, instruments such as vaccination and prevention policies are commonly used. But among wild animals these can hardly be implemented, [11]. However, it may be possible to try to contain a disease affecting a population by introducing in the environment another population which is a predator of the former. Whether this constitutes a feasible policy is another one of the possible questions that ecoepidemiology tries to answer. Some of these issues are illustrated in the first part of [16].

In the past decade research on what is now known as ecoepidemiology has progressed quite a lot. An increasing number of papers are devoted to the study of the relationships between demographic processes among different populations and diseases. Among the first papers that considered this problem the following ones are to be cited: [3, 5, 7]. In [18] the situation is considered in which the underlying demographic model is represented by a simple Lotka-Volterra system, with the shortcomings of presenting neutral type oscillations also in the ecoepidemic system. In [19, 21] this negative feature has been eliminated by considering quadratic intraspecific interactions. In these models however, persistent oscillations have not been found, while instead for competing species limit cycles have been shown to arise, [20]. A shortcoming of some of these oscillations is that they indicate that the ecosystem may be fragile, although the deterministic model prescribes that all the subpopulation survive. They may indeed attain very low levels, so that in practical situations where the environment could be subject to unforeseable fluctuations, for instance due to climatic changes, they may be completely wiped out, maybe causing irreversible damages to the ecosystem.

Since the literature on interacting populations is very rich, and more sophisticated models have been studied, also in the context of ecoepidemiology these have been considered, see for instance [1, 4], in which Holling type II and ratio-dependent models have been introduced. Ecoepidemic systems with the latter types of nonlinearities have been considered more recently,

[8, 9, 10]. Among the most interesting models related to food chains is the fairly recently proposed system (1), [2, 13]. Since it is claimed to provide a realistic description of ecological situations, it appears to be a viable starting point also for a more elaborated ecoepidemiological investigation. In fact the assumptions on which Holling type II models rest, is the fact that a return function cannot grow to infinity, but is bounded above. This corresponds to the fact that an individual can for instance feed up to a saturation value in spite of the abundant resources available.

In this paper therefore we introduce a contagious disease among the predators y in a predator-prey ecosystem, modelled via the following equations

$$\frac{dx}{dt} = a_1 x - b_1 x^2 - \frac{c_1 xy}{x + k_1}, \quad \frac{dy}{dt} = a_2 y - \frac{c_2 y^2}{x + k_2}. \tag{1}$$

This model incorporates a Holling type-II functional response and a modified version of the Leslie-Gower one, which as mentioned was introduced in the context of tritrophic food webs, [2, 13, 14, 17]. The global stability issue of a simpler predator-prey model with Leslie-Gower dynamics has been investigated in [12]. Note that in absence of prey, the predators still thrive at level $a_2 k_2 c_2^{-1}$, indicating the presence of other food sources.

In the growing ecoepidemic literature, from the early papers [5, 7], diseases mainly spreading in the prey are examined, [4, 19], but in [8, 10, 21] the epidemics is assumed to affect the predators. Here we reconsider this problem, looking at a more complicated model. In fact in [21] only quadratic interaction terms are considered, both of demographic as well as epidemics significance. With respect to [8] and [10] the main difference lies in introducing here intraspecific competition terms involving also the infected predators. These terms appear in the numerators of the predators' equations terms. The closest of the models is probably [8], but the predators interaction terms with prey differ, furthermore here we allow other food sources for the predators.

One of the main findings of this research is the conditions under which the coexistence equilibrium is globally asymptotically stable, i.e. it is the sole possible equilibrium to which from any initial condition the system will certainly evolve. In it the disease is of course endemic, so if the aim of let us say an ecologist or an administrator of a park is the disease eradication, then such conditions should be avoided. Conditions for the local asymptotic stability of boundary equilibria are established as well. In these, at least one subpopulation vanishes, so that if the aim instead is to remove either an obnoxious pest, via a disease, or another population, these other condi-

tions should instead be satisfied. The role of a intraspecific competition is highlighted: among sound predators it seems to lead to a disease-free environment, while for infected predators it may wipe out both prey and sound predators, leaving only the disease endemic in the predators, which seems to be a counterintuitive and interesting result.

The paper is organized as follows. We describe the ecoepidemic model in the next Section, then proceed to the difficult analysis of the coexistence equilibrium. Section 4 contains the stability and bifurcation analysis of the boundary equilibria. The persistence issue is next dealt with and we conclude the paper with a discussion of the results and comparison with former related findings.

2 The ecoepidemic model

We assume that the disease spreads only among the predators, and let y denote the susceptible predators and z the infected ones. The total predator population is $n(t) = y(t) + z(t)$. The disease transmission follows a simple mass action law with the disease incidence $\lambda > 0$. In the absence predators the prey population x grows logistically with intrinsic growth rate $a_1 > 0$ and carrying capacity $a_1 b_1^{-1}$. In contrast to [8], we also introduce intraspecific competition among the predators' sound and infected subpopulations, with parameters c_2 and c_3, for which $c_2 > c_3$.

The model reduces to the following set of autonomous nonlinear differential equations with nonnegative parameters

$$\begin{aligned} \frac{dx}{dt} &= a_1 x - b_1 x^2 - \frac{c_1 xy}{x + k_1} - \frac{p c_1 xz}{x + k_1}, \\ \frac{dy}{dt} &= a_2 y - \frac{c_2 y(y + z)}{x + k_2} - \lambda yz, \\ \frac{dz}{dt} &= \lambda yz + a_3 z - \frac{c_3 z(y + z)}{x + k_2}, \end{aligned} \tag{2}$$

where a_2, a_3, $a_2 \geq a_3$, are the per capita growth rates of each predator subpopulation. Thus from sick parents the disease can be transmitted to their offsprings. The parameters k_1, k_2 respectively represent the half saturation constants of the prey and predator populations. The Jacobian matrix of

system (2) is $J = (\alpha_{ij}) \in \mathbf{R}^{3\times 3}$, with entries

$$\alpha_{11} = a_1 - 2b_1x - \frac{c_1k_1(y+pz)}{(x+k_1)^2}, \quad \alpha_{12} = -\frac{c_1x}{(x+k_1)}, \quad \alpha_{13} = -\frac{c_1px}{(x+k_1)},$$
$$\alpha_{21} = \frac{c_2y(y+z)}{(x+k_2)^2}, \quad \alpha_{22} = a_2 - \lambda z - \frac{c_2(2y+z)}{(x+k_2)}, \quad \alpha_{23} = -\frac{c_2y}{(x+k_2)} - \lambda y,$$
$$\alpha_{31} = \frac{c_3z(y+z)}{(x+k_2)^2}, \quad \alpha_{32} = \lambda z - \frac{c_3z}{(x+k_2)}, \quad \alpha_{33} = a_3 - \frac{c_3(y+2z)}{(x+k_2)} + \lambda y.$$

By introducing the total environment population $\chi = x+y+z$, summing the equations (2) and bounding the right hand side from above, following the steps of [8], boundedness of the solution trajectories of this model is established. In particular,

$$\limsup_{t\to+\infty} x(t) \le \frac{a_1}{b_1} \equiv W_1, \quad \limsup_{t\to+\infty} \Big(y(t)+z(t)\Big) \le \frac{a_2(W_1+k_2)}{c_3} \equiv W_2. \quad (3)$$

In what follows, the system's equilibria are E_k and we denote by J_k and $\alpha_{ij}^{[k]}$ the Jacobian and its entries evaluated at E_k, $i = 1,2,3$, $j = 1,2,3$, $k = 1,2,3,4,5,6,7$.

3 The coexistence equilibrium

The ecosystem thrives at the point $E_5 \equiv (x_5, y_5, z_5)$, where

$$y_5 = \frac{-\lambda(x_5+k_2)a_3 + (a_2c_3 - a_3c_2)}{\lambda^2(x_5+k_2) + \lambda(c_2-c_3)}, \quad z_5 = \frac{\lambda(x_5+k_2)a_2 - (a_2c_3 - a_3c_2)}{\lambda^2(x_5+k_2) + \lambda(c_2-c_3)}$$

and x_5 is a the root of the following cubic

$$A_0x^3 + 3A_1x^2 + 3A_2x + A_3 = 0, \quad (4)$$

where

$$A_0 = \lambda^2 b_1, \quad 3A_1 = \lambda\Big(b_1(\lambda k_2 + c_2 - c_3) - \lambda(a_1 - b_1k_1)\Big),$$
$$A_2 = \lambda\Big((b_1k_1 - a_1)(\lambda k_2 + c_2 - c_3) - a_1k_1\lambda + c_1(pa_2 - a_3)\Big),$$
$$A_3 = a_1k_1\lambda(c_3 - \lambda k_2 - c_2) - c_1\lambda k_2(a_3 - pa_2) + c_1(1-p)(a_2c_3 - a_3c_2).$$

We consider only the case in which the equation (4) possesses exactly one real positive root. This occurs if $\widehat{G}^2+4\widehat{H}^3>0$ with $\widehat{G}=A_0^2A_3-3A_0A_1A_2+2A_1^3$ and $\widehat{H}=A_0A_2-A_1^2$. Denoting by n^* one of the cubic roots of $\frac{1}{2}[-\widehat{G}+\sqrt{\widehat{G}^2+4\widehat{H}^3}]$, Cardano's method gives then the root as $\frac{1}{A_0}[n^*-A_1-\widehat{H}/n^*]$. For feasibility of E_5, we need to ensure either one of the two sets of conditions

$$\frac{a_2c_3}{a_3}\geq\lambda(x_5+k_2)+c_2,\quad \lambda(x_5+k_2)+\max\left\{\frac{a_3c_2}{a_2},c_2\right\}>c_3; \tag{5}$$

$$\frac{a_2c_3}{a_3}\leq\lambda(x_5+k_2)+c_2,\quad \lambda(x_5+k_2)+\max\left\{\frac{a_3c_2}{a_2},c_2\right\}<c_3. \tag{6}$$

which give then restrictions on the root x_5.

Proposition 1. *E_5 is locally asymptotically stable if*

$$(a)\qquad \lambda z_5+b_1x_5+\frac{c_2(y_5+z_5)}{(x_5+k_2)}>\frac{c_1x_5(y_5+pz_5)}{(x_5+k_1)^2}+\frac{pc_1z_5}{(x_5+k_1)},$$

$$(b)\qquad \frac{c_3(y_5+z_5)}{(x_5+k_2)}+b_1x_5+\frac{c_1y_5}{(x_5+k_1)}>\lambda y_5+\frac{c_1x_5(y_5+pz_5)}{(x_5+k_1)^2},$$

$$(c)\qquad \lambda(c_2-c_3)x_5(y_5+z_5)<(a_2c_3-a_3c_2)(x_5+k_2),$$

$$(d)\qquad \frac{(x_5+k_2)\Big(c_1(y_5+pz_5)-b_1(x_5+k_1)^2\Big)\Big(\lambda(x_5+k_2)+c_2-c_3\Big)}{c_1(c_3-pc_2)(x_5+k_1)(y_5+z_5)}<-1.$$

Proof. We use the method of first approximation. We then have to show that the second compound matrix $J^{[2]}(E_5)$ of J_5 is stable and $\det(J_5)<0$.

Some of the entries of the Jacobian of (2) simplify at E_5 as follows:

$$\alpha_{11}^{[5]}=-x_5\Big(b_1-\frac{c_1(y_5+pz_5)}{(x_5+k_1)^2}\Big),\quad \alpha_{22}^{[5]}=-\frac{c_2y_5}{(x_5+k_2)},\quad \alpha_{33}^{[5]}=-\frac{c_3z_5}{(x_5+k_2)}.$$

Let us introduce the diagonal matrix $D=\mathrm{diag}(z_5,y_5,x_5)$. The matrix $J^{[2]}(E_5)$ is similar to $DJ^{[2]}(E_5)D^{-1}=(\beta_{ij})_{3\times3}$, and therefore $J^{[2]}(E_5)$ is stable if and only if $DJ^{[2]}(E_5)D^{-1}$ is stable. We have

$$\begin{aligned}
\beta_{11}&=\alpha_{11}^{[5]}+\alpha_{22}^{[5]},\quad \beta_{12}=\alpha_{23}^{[5]}\frac{z_5}{y_5},\ \beta_{13}=-\alpha_{13}^{[5]}\frac{z_5}{x_5},\\
\beta_{21}&=\alpha_{32}^{[5]}\frac{y_5}{z_5},\quad \beta_{22}=\alpha_{11}^{[5]}+\alpha_{33}^{[5]},\quad \beta_{23}=\alpha_{12}^{[5]}\frac{y_5}{x_5},\\
\beta_{31}&=-\alpha_{31}^{[5]}\frac{x_5}{z_5},\quad \beta_{32}=\alpha_{21}^{[5]}\frac{x_5}{y_5},\quad \beta_{33}=\alpha_{33}^{[5]}+\alpha_{22}^{[5]}.
\end{aligned}$$

Since the diagonal elements of $DJ^{[2]}(E_5)D^{-1}$ are negative, using Gershgorin's theorem the matrix is stable if it is row diagonally dominant. Let $G^* = \max\{R_1, R_2, R_3\}$, where

$$R_1 = \beta_{11} + \beta_{12} + \beta_{13} = -b_1 x_5 + \frac{c_1 x_5(y_5 + pz_5)}{(x_5 + k_1)^2} - \frac{c_2 y_5}{(x_5 + k_2)} - \left(\lambda + \frac{c_2}{(x_5 + k_2)}\right) z_5 + \frac{pc_1 z_5}{(x_5 + k_1)},$$

$$R_2 = \beta_{21} + \beta_{22} + \beta_{23} = \lambda y_5 + \frac{c_1 x_5(y_5 + pz_5)}{(x_5 + k_1)^2} - \frac{c_3(y_5 + z_5)}{(x_5 + k_2)} - \frac{c_1 y_5}{(x_5 + k_1)} - b_1 x_5,$$

$$R_3 = \beta_{31} + \beta_{32} + \beta_{33} = \frac{(c_2 - c_3)x_5(y_5 + z_5)}{(x_5 + k_2)^2} - \frac{(c_2 y_5 + c_3 z_5)}{(x_5 + k_2)}.$$

Now conditions (a), (b) and (c) imply indeed $G^* < 0$, i.e. diagonal dominance, which thus verifies stability. Further

$$\begin{aligned}\det(J_5) &= \alpha_{11}^{[5]}(\alpha_{22}^{[5]}\alpha_{33}^{[5]} - \alpha_{23}^{[5]}\alpha_{32}^{[5]}) - \alpha_{12}^{[5]}(\alpha_{21}^{[5]}b_{33}^{[5]} - \alpha_{31}^{[5]}\alpha_{23}^{[5]}) + \alpha_{13}^{[5]}(\alpha_{21}^{[5]}\alpha_{32}^{[5]} - \alpha_{31}^{[5]}\alpha_{22}^{[5]}) \\ &= -\lambda x_5 y_5 z_5 \Big[\Big(b_1 - \frac{c_1(y_5 + pz_5)}{(x_5 + k_1)^2}\Big)\Big(\lambda + \frac{c_2 - c_3}{(x_5 + k_2)}\Big) + \frac{c_1(pc_2 - c_3)(y_5 + z_5)}{(x_5 + k_2)^2(x_5 + k_1)}\Big].\end{aligned}$$

Condition (d) implies that $\det(J_5) < 0$, thus completing the proof. □

Proposition 2. *A sufficient condition for the equilibrium E_5 to be unstable is*

$$x_5\Big(b_1 - \frac{c_1(y_5 + pz_5)}{(x_5 + k_1)^2}\Big) + \frac{(a_2c_3 - a_3c_2)}{\lambda(x_5 + k_2)} < 0.$$

Proof. Since $c_2y_5 + c_3z_5 = \lambda^{-1}(a_2c_3 - a_3c_2)$, we have now

$$\begin{aligned}\mathrm{tr}(J_5) = \alpha_{11}^{[5]} + \alpha_{22}^{[5]} + \alpha_{33}^{[5]} &= -x_5\Big(b_1 - \frac{c_1(y_5 + pz_5)}{(x_5 + k_1)^2}\Big) - \frac{(c_2y_5 + c_3z_5)}{(x_5 + k_2)} \\ &= -\Big[x_5\Big(b_1 - \frac{c_1(y_5 + pz_5)}{(x_5 + k_1)^2}\Big) + \frac{(a_2c_3 - a_3c_2)}{\lambda(x_5 + k_2)}\Big]\end{aligned}$$

and the assumption implies $\mathrm{tr}(J_5) > 0$ and therefore instability of E_5. □

We now show the first main result of the paper.

Theorem 3.1. *The interior equilibrium E_5 is globally asymptotically stable if, recalling (3),*

$$b_1k_1(x_5+k_1) > c_1(y_5+pz_5), \tag{7}$$

$$c_3 > pc_2, \tag{8}$$

$$\frac{4b_1c_2}{(a_1+b_1k_1)}\Big[b_1 - \frac{c_1(y_5+pz_5)}{k_1(x_5+k_1)}\Big] > \Big[\frac{c_1}{k_1} + \frac{c_2(y_5+z_5)}{k_2(x_5+k_2)}\Big]^2, \tag{9}$$

$$\Big[\frac{pc_1}{(W_1+k_1)} - \frac{c_2(y_5+z_5)}{(x_5+k_2)k_2}\Big]^2 > \frac{4c_2}{k_2}\Big[b_1 - \frac{c_1(y_5+pz_5)}{(x_5+k_1)(W_1+k_1)}\Big], \tag{10}$$

$$\frac{pc_1}{(W_1+k_1)} > \frac{c_3(y_5+z_5)}{k_2(x_5+k_2)}. \tag{11}$$

Proof. Define the function $L(x,y,z) = L_1(x,y,z) + L_2(x,y,z) + L_3(x,y,z)$,

$$L_1 = x - x_5 - x_5\ln\frac{x}{x_5}, \quad L_2 = y - y_5 - y_5\ln\frac{y}{y_5}, \quad L_3 = z - z_5 - z_5\ln\frac{z}{z_5}.$$

We will show that L is a Lyapunov function. Easily, $L(x,y,z)$ vanishes at E_5 and it is positive for all $x,y,z>0$. Hence E_5 represents its global minimum.

Since the solutions of system (2) are bounded and ultimately enter a compact the set Σ, we can restrict the study of L to Σ. The time derivative of L_1 along the solutions of the system (2) can be determined using the linear algebraic system that defines E_5, to find

$$\frac{dL_1}{dt} = (x-x_5)\Big(a_1 - b_1x - \frac{c_1y}{(x+k_1)} - \frac{pc_1z}{(x+k_1)}\Big)$$

$$= (x-x_5)\Big[b_1x_5 + \frac{c_1y_5}{(x_5+k_1)} + \frac{pc_1z_5}{(x_5+k_1)} - b_1x - \frac{c_1y}{(x+k_1)} - \frac{pc_1z}{(x+k_1)}\Big]$$

$$= (x-x_5)\Big[\frac{c_1(y_5+pz_5)(x-x_5)}{(x_5+k_1)(x+k_1)} - b_1(x-x_5) - \frac{c_1(y-y_5)}{(x+k_1)} - \frac{pc_1(z-z_5)}{(x+k_1)}\Big].$$

Similarly,

$$\frac{dL_2}{dt} = (y-y_5)\Big(a_2 - \frac{c_2(y+z)}{(x+k_2)} - \lambda z\Big)$$
$$= (y-y_5)\Big[\lambda z_5 + \frac{c_2(y_5+z_5)}{(x_5+k_2)} - \frac{c_2(y+z)}{(x+k_2)} - \lambda z\Big]$$
$$= (y-y_5)\Big[-\lambda(z-z_5) + \frac{c_2(y_5+z_5)(x-x_5)}{(x_5+k_2)(x+k_2)} - \frac{c_2\Big((y-y_5)+(z-z_5)\Big)}{(x+k_2)}\Big];$$
$$\frac{dL_3}{dt} = (z-z_5)\Big(a_3 - \frac{c_3(y+z)}{(x+k_2)} + \lambda y\Big)$$
$$= (z-z_5)\Big[-\lambda y_5 + \frac{c_3(y_5+z_5)}{(x_5+k_2)} - \frac{c_3(y+z)}{(x+k_2)} + \lambda y\Big]$$
$$= (z-z_5)\Big[\lambda(y-y_5) + \frac{c_3(y_5+z_5)(x-x_5)}{(x_5+k_2)(x+k_2)} - \frac{c_3\Big((y-y_5)+(z-z_5)\Big)}{(x+k_2)}\Big].$$

Adding these contributions, for $\mathbf{v} = \Big((x-x_5),(y-y_5),(z-z_5)\Big)^T$ we find

$$\frac{dL}{dt} = A(x-x_5)^2 + B(y-y_5)^2 + C(z-z_5)^2 + 2H(x-x_5)(y-y_5)$$
$$+2F(y-y_5)(z-z_5) + 2G(z-z_5)(x-x_5) = -\mathbf{v}^T Q\mathbf{v}. \qquad (12)$$

Here Q is the symmetric quadratic form given by

$$Q = \begin{bmatrix} A & H & G \\ H & B & F \\ G & F & C \end{bmatrix},$$

with entries that are functions only of the variable x,

$$A = b_1 - \frac{c_1(y_5+pz_5)}{(x_5+k_1)(x+k_1)}, \quad B = \frac{c_2}{x+k_2}, \quad C = \frac{c_3}{x+k_2}, \quad F = \frac{1}{2}\frac{c_2+c_3}{x+k_2},$$
$$H = \frac{1}{2}\Big[\frac{c_1}{x+k_1} - \frac{c_2(y_5+z_5)}{(x_5+k_2)(x+k_2)}\Big], \quad G = \frac{1}{2}\Big[\frac{pc_1}{x+k_1} - \frac{c_3(y_5+z_5)}{(x_5+k_2)(x+k_2)}\Big].$$

Thus if the matrix Q is positive definite then $\frac{dL}{dt} < 0$. We need all of the principal minors of Q namely $P_1 \equiv A$, $P_2 \equiv AB - H^2$, $P_3 \equiv ABC + 2FGH - AF^2 - BG^2 - CH^2$, to be positive, i.e.

$$P_1 = b_1 - \frac{c_1(y_5 + pz_5)}{(x_5 + k_1)(x + k_1)} > 0,$$

$$P_2 = \Big[b_1 - \frac{c_1(y_5 + pz_5)}{(x_5 + k_1)(x + k_1)}\Big]\frac{c_2}{x + k_2} - \frac{1}{4}\Big[\frac{c_1}{x + k_1} - \frac{c_2(y_5 + z_5)}{(x_5 + k_2)(x + k_2)}\Big]^2 > 0,$$

$$P_3 = C(AB - H^2) + G(FH - BG) + F(GH - AF) > 0.$$

Now for P_1, differentiating A with respect to x,

$$\frac{dA}{dx} = \frac{c_1(y_5 + pz_5)}{(x_5 + k_1)(x + k_1)^2} > 0,$$

we find that it is a monotonic increasing function, hence by (7),

$$A(x) > A(0) = b_1 - \frac{c_1(y_5 + pz_5)}{(x_5 + k_1)k_1} > 0.$$

Using this result and (9), for P_2 we find

$$\begin{aligned} P_2 &= \Big[b_1 - \frac{c_1(y_5 + pz_5)}{(x_5 + k_1)(x + k_1)}\Big]\frac{c_2}{x + k_2} - \frac{1}{4}\Big[\frac{c_1}{x + k_1} + \frac{c_2(y_5 + z_5)}{(x_5 + k_2)(x + k_2)}\Big]^2 \\ &> \Big[b_1 - \frac{c_1(y_5 + pz_5)}{(x_5 + k_1)k_1}\Big]\frac{c_2}{\frac{a_1}{b_1} + k_2} - \frac{1}{4}\Big[\frac{c_1}{k_1} + \frac{c_2(y_5 + z_5)}{(x_5 + k_2)k_2}\Big]^2 > 0. \end{aligned}$$

For P_3 we have by (8)

$$\begin{aligned} FH - BG = \frac{1}{2(x + k_2)}\Big\{\frac{(c_2 + c_3)}{2}\Big[\frac{c_1}{(x + k_1)} - \frac{c_2(y_5 + z_5)}{(x_5 + k_2)(x + k_2)}\Big] \\ -c_2\Big[\frac{pc_1}{(x + k_1)} - \frac{c_3(y_5 + z_5)}{(x_5 + k_2)(x + k_2)}\Big]\Big\} > \frac{c_1(c_3 - pc_2)}{2(x + k_1)(x + k_2)} > 0. \end{aligned}$$

Now $G > 0$, entailing $G(FH - BG) > 0$, since, recalling the upper bounds (3), and (11)

$$G > \frac{1}{2}\Big[\frac{pc_1}{(W_1 + k_1)} - \frac{c_3(y_5 + z_5)}{(x_5 + k_2)k_2}\Big].$$

For P_3 using (10) we have,

$$GH - AF = \frac{1}{4}\Big[\frac{pc_1}{(x+k_1)} - \frac{c_3(y_5+z_5)}{(x_5+k_2)(x+k_2)}\Big]\Big[\frac{c_1}{(x+k_1)} - \frac{c_2(y_5+z_5)}{(x_5+k_2)(x+k_2)}\Big]$$
$$-\frac{c_2+c_3}{2(x+k_2)}\Big[b_1 - \frac{c_1(y_5+pz_5)}{(x_5+k_1)(x+k_1)}\Big]$$
$$> \frac{1}{4}\Big[\frac{pc_1}{(x+k_1)} - \frac{c_2(y_5+z_5)}{(x_5+k_2)(x+k_2)}\Big]^2 - \frac{c_2+c_3}{2(x+k_2)}\Big[b_1 - \frac{c_1(y_5+pz_5)}{(x_5+k_1)(x+k_1)}\Big]$$
$$> \frac{1}{4}\Big[\frac{pc_1}{(W_1+k_1)} - \frac{c_2(y_5+z_5)}{(x_5+k_2)k_2}\Big]^2 - \frac{c_2}{k_2}\Big[b_1 - \frac{c_1(y_5+pz_5)}{(x_5+k_1)(W_1+k_1)}\Big] > 0.$$

Combining these results it follows that $P_3 > 0$. Hence the symmetric matrix Q is positive definite, implying $\frac{dL}{dt} < 0$ along the trajectories. Thus L is a Lyapunov function, and global stability for E_5 follows. □

4 The boundary equilibria

The system's equilibria in which at least one subpopulation vanishes are the origin E_0 and the points $E_i \equiv (x_i, y_i, z_i)$, $i = 1, \ldots, 4, 6, 7$. In particular

$$E_1 \equiv \left(\frac{a_1}{b_1}, 0, 0\right), \quad E_6 \equiv \left(0, \frac{a_2k_2}{c_2}, 0\right), \quad E_7 \equiv \left(0, 0, \frac{a_3k_2}{c_3}\right)$$
$$E_4 \equiv \left(0, \frac{(a_2c_3 - a_3c_2) - \lambda k_2 a_3}{\lambda(\lambda k_2 + c_2 - c_3)}, \frac{\lambda k_2 a_2 - (a_2c_3 - a_3c_2)}{\lambda(\lambda k_2 + c_2 - c_3)}\right)$$

while $z_2 = 0$ and $y_3 = 0$ characterize the remaining equilibria.

Since the algebraic system from (2) with $z_2 = 0$ reduces to the quadratic

$$b_1c_2x_2^2 + (c_2b_1k_1 - c_2a_1 + c_1a_2)x_2 + c_1a_2k_2 - c_2a_1k_1 = 0,$$

by Descarte's rule there is one positive root if

$$a_1 > \frac{c_1a_2k_2}{k_1c_2} \equiv a^{[6]} \tag{13}$$

Letting $\Gamma = c_2b_1k_1 - c_2a_1 + c_1a_2$ the equilibrium E_2 is given by

$$x_2 = \frac{-\Gamma + \sqrt{\Gamma^2 - 4b_1c_2(c_1a_2k_2 - c_2a_1k_1)}}{2b_1c_2}; \quad y_2 = \frac{a_2(x_2+k_2)}{c_2}.$$

Proceeding similarly for E_3 setting $\Theta = b_1c_3k_1 + pc_1a_3 - c_3a_1$, we have

$$x_3 = \frac{-\Theta + \sqrt{\Theta^2 - 4b_1c_3(pc_1a_3k_2 - c_3a_1k_1)}}{2b_1c_3}; \quad z_3 = \frac{a_3(x_3 + k_2)}{c_3}.$$

The prey-free equilibrium E_4 is feasible if

$$\frac{(a_2c_3 - a_3c_2)}{a_2k_2} < \lambda < \frac{(a_2c_3 - a_3c_2)}{a_3k_2}. \tag{14}$$

The equilibrium E_2 is feasible if (13) holds and E_3 is feasible for

$$a_1 > \frac{pc_1a_3k_2}{k_1c_3} \equiv a^{[7]} \tag{15}$$

4.1 Stability

The equilibria E_0 and E_1 are both unstable, since their eigenvalues are a_1, a_2 and a_3 and $-a_1$, a_2 and a_3 respectively.

The equilibrium E_6 is locally asymptotically stable for

$$a_1 < a^{[6]}, \quad \lambda < \frac{(a_2c_3 - a_3c_2)}{a_2k_2} \equiv \lambda^{[6]}, \tag{16}$$

since the eigenvalues of the Jacobian in this case are $a_1 - a^{[6]}$, $-a_2$ and $c_2^{-1}[\lambda a_2k_2 - (a_2c_3 - a_3c_2)]$.

Similarly, E_7 is locally asymptotically stable if

$$a_1 < a^{[7]}, \quad \lambda > \frac{(a_2c_3 - a_3c_2)}{a_3k_2} \equiv \lambda^{[7]}. \tag{17}$$

At E_2 the Jacobian factors giving the quadratic

$$\eta^2 - \eta\left(\alpha_{11}^{[2]} + \alpha_{22}^{[2]}\right) + \alpha_{11}^{[2]}\alpha_{22}^{[2]} - \alpha_{12}^{[2]}\alpha_{21}^{[2]} = 0,$$

and one explicit eigenvalue, $\alpha_{33}^{[2]} = \lambda y_2 - c_2^{-1}(a_2c_3 - a_3c_2)$, with $\alpha_{22}^{[2]} = -a_2 < 0$,

$$\alpha_{11}^{[2]} = x_2\Big(\frac{c_1a_2(x_2 + k_2)}{c_2(x_2 + k_1)^2} - b_1\Big), \quad \alpha_{12}^{[2]} = -\frac{c_1x_2}{x_2 + k_1} < 0, \quad \alpha_{21}^{[2]} = \frac{a_2^2}{c_2} > 0.$$

Therefore the conditions for stability are

$$\lambda < \frac{a_2c_3 - a_3c_2}{a_2(x_2 + k_2)} = \lambda^{[2]} < 0, \quad \frac{c_1a_2(x_2 + k_2)}{b_1c_2(x_2 + k_1)^2} < 1. \tag{18}$$

In a similar way we find at E_3 another quadratic is obtained,

$$\eta^2 - \eta\left(\alpha_{11}^{[3]} + \alpha_{33}^{[3]}\right) + \alpha_{11}^{[3]}\alpha_{33}^{[3]} - \alpha_{13}^{[3]}\alpha_{31}^{[3]} = 0,$$

and one eigenvalue is explicitly $\alpha_{22}^{[3]}$ with $\alpha_{33}^{[3]} = -a_3$, $\alpha_{31}^{[3]} = c_3^{-1}a_3^2$ and

$$\alpha_{22}^{[3]} = \frac{a_2c_3 - a_3c_2}{c_3} - \lambda z_3, \quad \alpha_{11}^{[3]} = x_3\Big[\frac{pc_1a_3(x_3+k_2)}{c_3(x_3+k_1)^2} - b_1\Big], \quad \alpha_{13}^{[3]} = \frac{-pc_1x_3}{x_3+k_1} < 0.$$

Hence E_3 is locally asymptotically stable if

$$\lambda > \frac{a_2c_3 - a_3c_2}{a_3(x_3+k_2)} = \lambda^{[3]}, \quad \frac{pc_1a_3(x_3+k_2)}{b_1c_3(x_3+k_1)^2} < 1. \tag{19}$$

In a similar way at E_4 the eigenvalue $\alpha_{11}^{[4]} = a_1 - k_1^{-1}c_1(y_4 + pz_4)$ is easily obtained from the factorization of the Jacobian. Also $\alpha_{22}^{[4]} = -k_2^{-1}c_2y_4 < 0$, $\alpha_{33}^{[4]} = -k_2^{-1}c_3z_4 < 0$ and

$$\alpha_{23}^{[4]} = -y_4\left(\lambda + \frac{c_2}{k_2}\right) < 0, \quad \alpha_{32}^{[4]} = z_4\left(\lambda - \frac{c_3}{k_2}\right).$$

The Routh-Hurwitz criterion on the resulting quadratic provides the remaining stability condition $\alpha_{32}^{[4]} > 0$, i.e.

$$\lambda > \frac{c_3}{k_2}, \quad y_4 + pz_4 > \frac{a_1k_1}{c_1}. \tag{20}$$

4.2 Bifurcations

In view of the structure of the Jacobian which factors at the three equilibria E_2, E_3, E_4, in order to obtain complex conjugate pairs of eigenvalues at these equilibria it is enough to annihilate the linear term in η, thus to require respectively

$$\alpha_{11}^{[2]} + \alpha_{22}^{[2]} = 0, \quad \alpha_{11}^{[3]} + \alpha_{33}^{[3]} = 0, \quad \alpha_{22}^{[4]} + \alpha_{33}^{[4]} = 0.$$

But in the latter case $\alpha_{22}^{[4]} + \alpha_{33}^{[4]} < 0$ so that it is not possible to satisfy the condition. Thus at E_4 no Hopf bifurcation can arise. The Hopf bifurcations are instead also shown graphically by numerical simulations, Figures 2, 4.

5 Persistence

If a compact set $D \subset \Omega = \{(x, y, z); x > 0, y > 0, z > 0\}$ exists such that all solutions of (2) eventually enter and remain in D, the system is called persistent.

Proposition 3. *The system (2) is persistent if*

$$(i) \quad c_3 z_3 < \frac{a_2 c_3 - a_3 c_2}{\lambda} < c_2 y_2, \quad (ii) \quad y_4 + p z_4 < \frac{a_1 k_1}{c_1},$$
$$(iii) \quad a_1 > a^{[6]}, \quad \lambda > \lambda^{[6]}, \quad (iv) \quad a_1 > a^{[7]}, \quad \lambda < \lambda^{[7]}.$$

Proof. We use the method of average Lyapunov function, see [6], considering a function of the form

$$V(x, y, z) = x^{\gamma_1} y^{\gamma_2} z^{\gamma_3},$$

where γ_i, $i = 1, 2, 3$ are positive constants to be determined. We define

$$\begin{aligned} \Pi(x, y, z) &= \frac{\dot{V}}{V} \\ &= \gamma_1\Big(a_1 - b_1 x - \frac{c_1 y}{(x + k_1)} - \frac{p c_1 z}{(x + k_1)}\Big) + \gamma_2\Big(a_2 - \frac{c_2(y + z)}{(x + k_2)} - \lambda z\Big) \\ &\quad + \gamma_3\Big(a_3 - \frac{c_3(y + z)}{(x + k_2)} + \lambda y\Big). \end{aligned}$$

We now prove that this function is positive at each boundary equilibrium. In fact at E_0 and E_1 we have $\Pi(0, 0, 0) = \gamma_1 a_1 + \gamma_2 a_2 + \gamma_3 a_3 > 0$ and $\Pi(x_1, 0, 0) = \gamma_2 a_2 + \gamma_3 a_3 > 0$ respectively. Moreover, from condition (i), we find

$$\Pi(x_2, y_2, 0) = \gamma_3(\lambda y_2 - \frac{a_2 c_3 - a_3 c_2}{c_2}) > 0,$$
$$\Pi(x_3, 0, z_3) = \gamma_2(\frac{a_2 c_3 - a_3 c_2}{c_2} - \lambda z_3) > 0.$$

From condition (ii) instead we have

$$\Pi(0, y_4, z_4) = \frac{\gamma_1 c_1}{k_1}\Big(\frac{a_1 k_1}{c_1} - \frac{y_4 + p z_4}{k_1}\Big) > 0,$$

while condition (iii) entails

$$\Pi(0, y_6, 0) = \gamma_1\Big(a_1 - \frac{c_1 a_2 k_2}{c_2 k_1}\Big) + \gamma_3\Big(\frac{\lambda a_2 k_2}{c_2} - \frac{(a_2 c_3 - a_3 c_2)}{c_2}\Big) > 0.$$

Finally

$$\Pi(0,0,z_7) = \gamma_1\Big(a_1 - \frac{pc_1a_3k_2}{c_3k_1}\Big) + \gamma_2\Big(\frac{(a_2c_3 - a_3c_2)}{c_3} - \frac{\lambda a_3k_2}{c_3}\Big) > 0$$

follows by condition (iv). Hence γ_1, γ_2, γ_3 can be chosen to ensure $\Pi > 0$ at the boundary equilibria. Hence V is an average Lyapunov function and thus the system (2) is persistent. □

6 Discussion

Our numerical simulations illustrate the theoretical findings. The equilibrium E_2 is in fact attained, Figure 1 and the bifurcation in the two-dimensional prey susceptible-predator phase plane $x-y$ is pictorially described by Figure 2. The stable behavior at equilibrium E_3 is shown in Figure 3. The limit cycle after bifurcation appears instead in Figure 4. Figure 5 shows instead the system's trajectories settling to equilibrium E_4. The coexistence equilibrium point E_5 has indeed been found via numerical simulations, see Figure 6, and its global asymptotical stability is depicted in Figure 7.

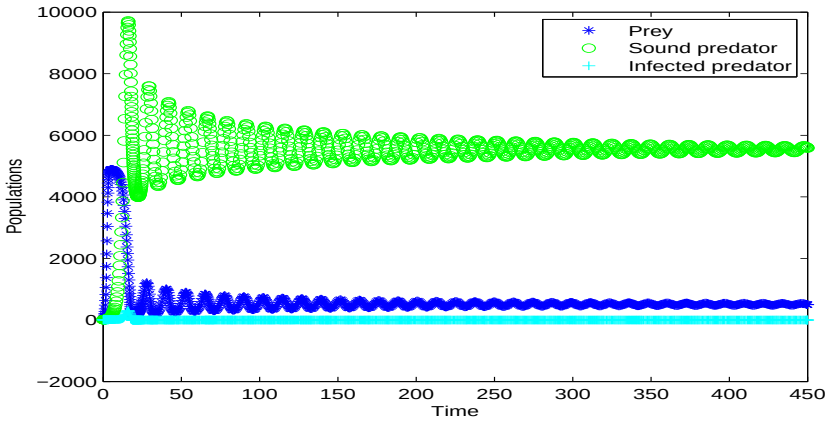

Figure 1: Stable equilibrium E_2 for the parameter values: $a_1 = 2.46$, $b_1 = 0.0005$, $a_2 = 0.5$, $c_1 = 0.6$, $c_2 = 0.1$, $c_3 = 0.5$, $a_3 = 0.1$, $\lambda = 0.0002$, $p = 0.05$, $k_1 = 1000$, $k_2 = 600$.

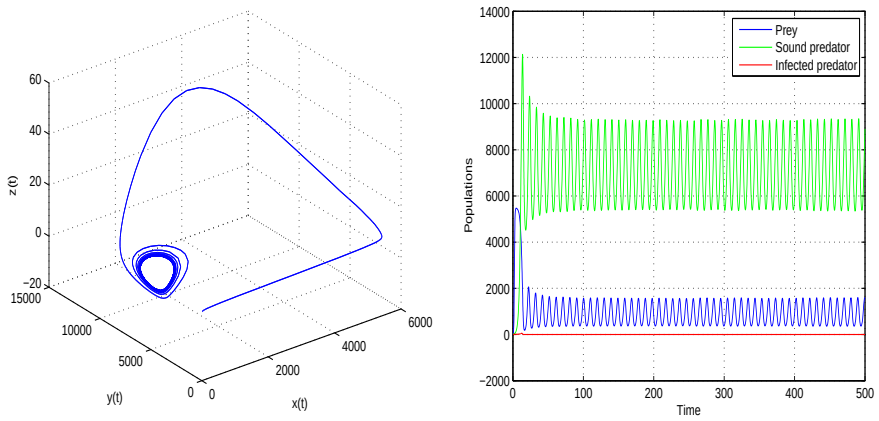

Figure 2: Hopf bifurcation at E_2 for the parameter values: $a_1 = 2.749694$, $b_1 = 0.0005$, $a_2 = 0.60$, $c_1 = 0.6$, $c_2 = 0.12$, $c_3 = 0.8$, $a_3 = 0.1$, $\lambda = 0.0002$, $p = 0.05$, $k_1 = 1000$, $k_2 = 600$.

Interpreting our results, we find that the ecosystem cannot collapse, nor can the prey alone survive, in view of the instability of E_0 and E_1. The predators-only equilibria can be attained, since other food sources are allowed in the underlying model (1), with a low enough prey reproduction rate, and respectively either a low enough disease incidence, (16) for the disease-free E_6, or a high one, (17) for the pandemic equilibrium E_7. Note also that E_2 and E_6 are incompatible, i.e. if E_2 is feasible, E_6 must be unstable, and vice versa, compare (13) and (16). Similarly behaves the pair E_3 and E_7, from (15) and (17). The prey-free equilibrium E_4 has the disease endemic in the predators, and can be attained for a reasonably high disease incidence, (20). It is not possible to find limit cycles around it.

Comparison with [8] shows that here more equilibria are found, namely E_3, E_5, E_6, and E_7. While here E_1 is inconditionally unstable, in [8] it can be stabilized under suitable conditions and becomes even globally asymptotically stable. The Hopf bifurcation at E_2 is common in both models, as it pertains to the demographic model upon which the ecoepidemics is built. The predators-only endemic equilibrium exists and is stable in both cases. The coexistence equilibrium in [8] is shown only to be locally asymptotically stable.

In [10] note that E_5, E_6, and E_7 are absent. Again in [10] E_1, E_2, E_3

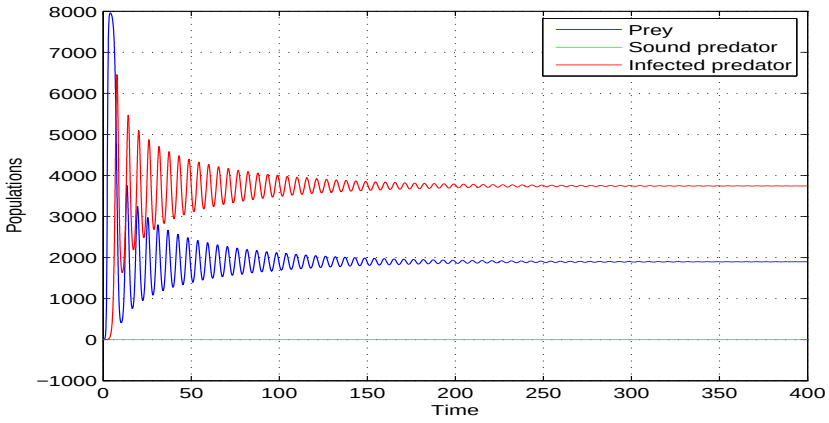

Figure 3: Stable equilibrium E_3 for the parameter values: $a_1 = 4.0$, $b_1 = 0.0005$, $a_2 = 0.3$, $c_1 = 2.1$, $c_2 = 0.1$, $c_3 = 1.0$, $a_3 = 1.5$, $\lambda = 0.0217$, $p = 0.93$, $k_1 = 500$, $k_2 = 600$.

and E_4 could be stabilized, by suitable parameter combinations; this is to be compared to similar results holding for (2), but in contrast with the instability of E_1 of this model. In [10] also sufficient conditions are identified for which the ecosystem does not collapse, while here the unconditional instability of the origin prevents it always. The global asymptotic stability of the coexistence equilibrium holds in [10] and here as well, but the proofs use different techniques.

Thus the results compared to former findings are quite close, but in general, the conditions ensuring these properties are more strict in the present model, since they intrinsically contain the intraspecific competition parameters. The main conclusion of this study enlightens the role that the intraspecific competition plays in fighting the disease, which is a relevant issue in epidemiology, [15]. Note in fact that a large c_2 renders the disease-free equilibrium E_2 feasible, (13), while at the same time making $\lambda^{[2]} < 0$, and the second condition (18) verified, thus rendering E_2 also stable. Similarly, it makes $\lambda^{[7]} < 0$, thus to prevent E_7 to be stable, so that the epidemics spreads to the whole predators, and the prey are wiped out, we need a very small value of c_3, (17). Therefore a high competition among sound predators seems to lead to a disease-free environment, while a high competition among infected predators may have the consequence of wiping out both prey

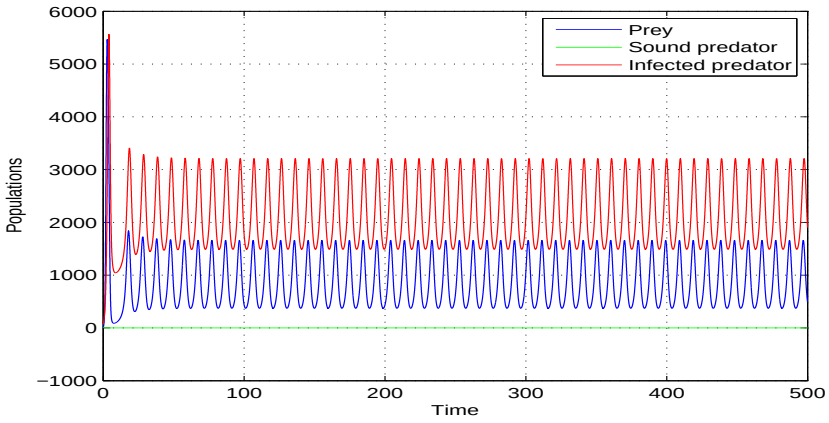

Figure 4: Hopf bifurcation at E_3 for the parameter values: $a_1 = 3.6$, $b_1 = 0.0005$, $a_2 = 0.3$, $c_1 = 2.1$, $c_2 = 0.1$, $c_3 = 1.0$, $a_3 = 1.5$, $\lambda = 0.0217$, $p = 0.93$, $k_1 = 500$, $k_2 = 600$; and initial condition $(14, 10, 70)$.

and sound predators, leaving only the infected predators as survivors in the ecosystem. This appears to be quite a counterintuitive and interesting result.

References

[1] Arino, O., Abdllaoui, A. E., Mikram, J., Chattopadhyay, J., (2004) Infection in prey population may act as biological control in ratio-dependent predator-prey models, *Nonlinearity* **17**, 1101-1116.

[2] Aziz-Alaoui, M. A., (2002) Study of a Leslie-Gower-type tritrophic population. *Chaos Solitons and Fractals.* **14(8)**, 1275-1293.

[3] Beltrami, E., Carroll, T.O., (1994) Modelling the role of viral disease in recurrent phytoplankton blooms, *J. Math. Biol.* **32**, 857-863.

[4] Chattopadhyay, J., Arino, O., (1999) A predatorprey model with disease in the prey, *Nonlinear Anal.* **36**, 747-766.

[5] Freedman, H. I., (1990) A model of predator -prey dynamics modified by the action of parasite. *Math. Biosci.* **99**, 143-155.

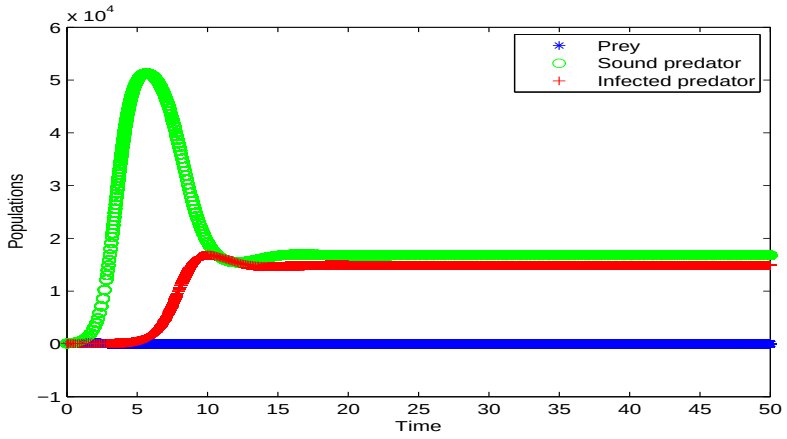

Figure 5: Local stability of the dynamical system (2) at E_4 for the parameter values: $a_1 = 0.5$, $b_1 = 0.0005$, $a_2 = 1.8$, $c_1 = 0.6$, $c_2 = 0.05$, $c_3 = 0.04$, $a_3 = 0.005$, $\lambda = 0.00005$, $p = 0.7$, $k_1 = 2000$, $k_2 = 1500$.

[6] Gard, T. C., Hallam, T.G., (1979) Persistence in Food web-1, Lotka-Volterra food chains. *Bull. Math. Biol.* **41**, 877-891.

[7] Hadeler, K. P., Freedman, H. I., (1989) Predator-prey populations with parasitic infection. *J. Math. Biol.* **27**, 609-631.

[8] Haque, M., Venturino, E., (2006) Increase of the prey may decrease the healthy predator population in presence of a disease in the predator, *HERMIS* **7**, 39-60.

[9] Haque, M., Venturino, E., (2006) The role of transmissible diseases in the Holling-Tanner predator-prey model, *Theoretical Population Biology* **70**, 273-288.

[10] Haque, M., Venturino, E., (2007) An ecoepidemiological model with disease in the predator; the ratio-dependent case, *Math. Meth. Appl. Sci.* **30**, 1791-1809.

[11] Hethcote, H. W., (2000) The mathematics of infectious diseases. *SIAM Rev.* **42**, 599-653.

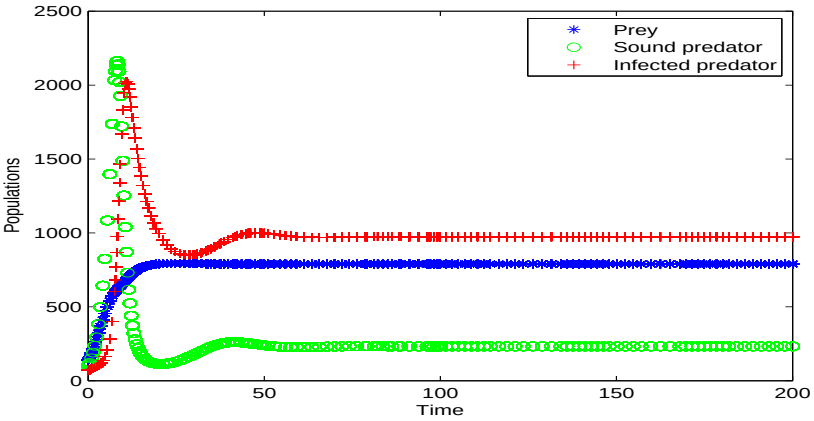

Figure 6: Coexistence equilibrium E_5 for the parameter values: $a_1 = 0.4$, $b_1 = 0.0005$, $a_2 = 0.5$, $c_1 = 0.06$, $c_2 = 0.03$, $c_3 = 0.5$, $a_3 = 0.1$, $\lambda = 0.0005$, $p = 0.003$, $k_1 = 2000$, $k_2 = 2000$.

[12] Korobeinikov, A., (2001) A Lyapunov function for Leslie-Gower prey-predator models. *Appl. Math. Lett.* **14(6)**, 697-699.

[13] Letellier, C., Aziz-Alaoui, M. A., (2002) Analysis of the dynamics of a realistic ecological model. *Chaos Solitons and Fractals.* **13(1)**, 95-107.

[14] Letellier, C., Aguirre, L., Maquet, J., Aziz-Alaoui, M. A., (2002) Should all the species of a food chain be counted to investigate the global dynamics. *Chaos Solitons and Fractals.* **13(5)**, 1099-1113.

[15] Liu R., Duvvuri V. R. S. K., Wu J., (2008) Spread pattern formation of H5N1-avian influenza and its implications for control strategies, *Math. Model. Nat. Phenom.* **3 (7)**, 161-179.

[16] H. Malchow, S. Petrovskii, E. Venturino, Spatiotemporal patterns in Ecology and Epidemiology, CRC, 2008, 442 pp.

[17] Upadhyay, R. K., Rai, V., (1997) Why chaos is rarely observed in natural population. *Chaos Solitons and Fractals.* **8(12)**, 1933-1939.

[18] Venturino, E., (1994), The influence of diseases on Lotka Volterra systems, *Rocky Mountain Journal of Mathematics*, **24**, 381-402.

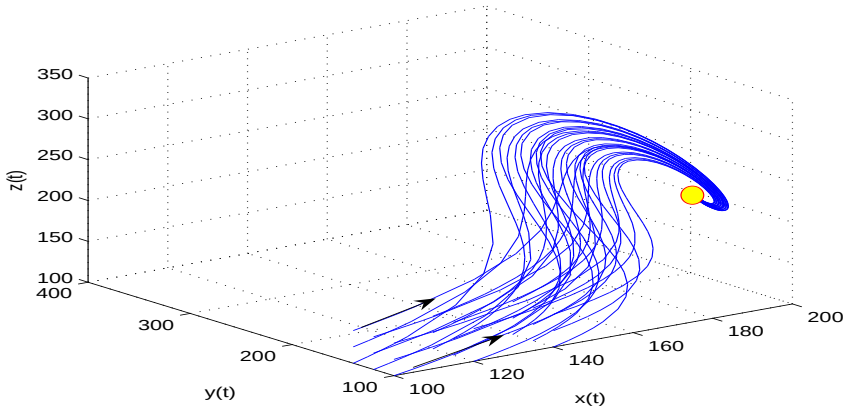

Figure 7: Illustration of global stability for the coexistence equilibrium E_5 for the parameter values: $a_1 = 2.0$, $b_1 = 0.01$, $a_2 = 1.2; a_3 = 0.2$, $c_1 = 0.7$, $c_2 = 0.1$, $c_3 = 2.1$, $\lambda = 0.005$, $p = 0.5$, $k_1 = 1000$, $k_2 = 700$.

[19] Venturino, E., (1995) Epidemics in predator-prey models: disease among the prey, in O. Arino, D. Axelrod, M. Kimmel, M. Langlais (Editors): *Mathematical Population Dynamics: Analysis of Heterogeneity, Vol. 1: Theory of Epidemics*, Wuertz Publ. Ltd, Winnipeg, Canada, p. 381-393.

[20] Venturino, E., (2001), The effects of diseases on competing species, *Math. Biosc.* **174**, 111-131.

[21] Venturino, E., (2002) Epidemics in predator-prey models: disease in the predators, *IMA J. of Mathematics Applied in Medicine and Biology* **19**, 185-205.